

ISLAND BIOGEOGRAPHY OF ANTS

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The renewed interest in island biogeography during the last decade has stemmed in part from the fact that islands represent biological microcosms where ecological and evolutionary phenomena can be observed more readily than on continents. Along with the new focus on species-area relations provided by MacArthur and Wilson (1963, 1967) and Hamilton and Rubinoff (1963) came the idea that ecological mechanisms basic to all communities could best be elucidated in the simple communities present on islands.

This study was undertaken as part of a general analysis of niche segregation and habitat utilization in a north temperate zone ant community. It was found that the factors important to niche segregation and community structure were also the controlling factors in the species-area relationship. This report will describe how the geographical distribution of a physical parameter (temperature), of demonstrated physiological significance to the taxon studied, can be used to predict the number of species that an area of land will contain.

The Study Areas

The study was conducted entirely within Branford and Guilford Townships in New Haven County, Connecticut (Fig. 1). These two adjacent townships are located at the southern border of Connecticut where its coast forms the northern border of Long Island Sound, a long (196 km), shallow arm of the Atlantic Ocean extending largely in an east to west direction. The Branford-Guilford section of the Connecti-

cut Coast is rockbound (Sharp, 1929); the very irregular features of the current coastline are largely determined by the presence of exposed bedrock which was scraped bare by the last glacial advance. It is an area of thin, podzolic soils, and prior to alteration by man the soil was generously dotted with boulders and the smaller transported materials associated with glaciation. From this surficial geological history results a relatively irregular topography and considerable heterogeneity of the soil-surface environment.

Just at the Branford-Guilford border two parallel rocky ridges project out at an angle of 40° for about 2 km into Long Island Sound. Most of these ridge lines are sunken, but the tops of the hills remain as The Thimble Islands. These range in size from bare rocks a few square meters (m²) in extent and barely reaching above the water's surface at high tide, to Horse Island which is more than 4 hectares (ha) in extent and rises to about 15 meters above sea-level. The vegetation of the study areas ranges from a sparse low field layer of pioneer species growing in rock cracks and presumably exposed to salt spray, to dense oak-hickory woodland. Four zones identifiable along this continuum, were dominated by the following plants: 1) *Solidago sempervirens-Rhus radicans*; 2) *Juniperus virginiana-Myrica pensylvanica*; 3) *Pinus ridiga-Gaylussacia baccata*; 4) *Carya* sp.-*Quercus* spp.

Soil depth and soil quality coupled with physiological dryness of the habitat due to wind and salt spray were thought to be the controlling elements along this continuum. Within the study areas this continuum expressed itself in three geographical patterns: 1) smaller islands had lower and

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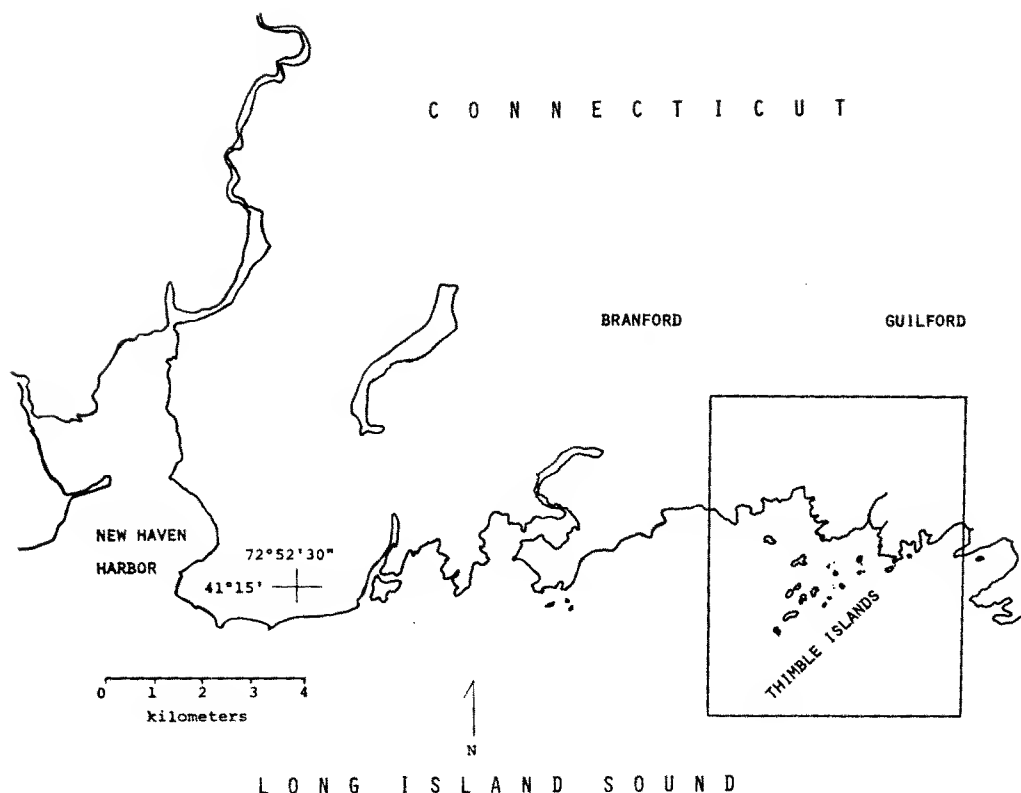


FIG. 1. The Connecticut coast east of New Haven. The rectangle encloses the study areas shown in detail in Fig. 2.

less dense vegetation than larger islands; 2) islands farther from the mainland had lower and less dense vegetation than closer islands due to increased exposure; and 3) the 'edges' of the study areas where they bordered salt water, had lower and less dense vegetation than the interiors of the study areas.

The area of the coast where the islands originate is marked by salt marshes which fill the shallower and more protected bays, and which along with land fill in the Leete's Island area, obscure the natural topography of the region. The details of this human influence are known, and Flint (1964, 1971) has published detailed maps which show the surficial geology in its unaltered state (see inset Fig. 2). Flint's work makes it clear that all three types of sites included in this study, the islands, the islands in

the marsh, and the coastal section, are not only a part of the same bedrock ridgeline, but are extremely similar in that the surface of all of them is made up largely of exposed bedrock and glacial till. Thus no major differences in soils could be detected between different study areas. Figure 2 presents a detailed map of the study areas, and Table 1 the basic data for each of the 9 islands, 3 islands in the marsh, 3 transects and 1 coastal area. All the study areas are contained within a rectangular area about 4 km long and 1 km wide, whose long axis parallels The Thimble Islands Chain.

The Ant Survey

Ant collecting was carried on in the study areas in 1971 and 1972 during daylight hours between 6 a.m. and 8 p.m. Stray

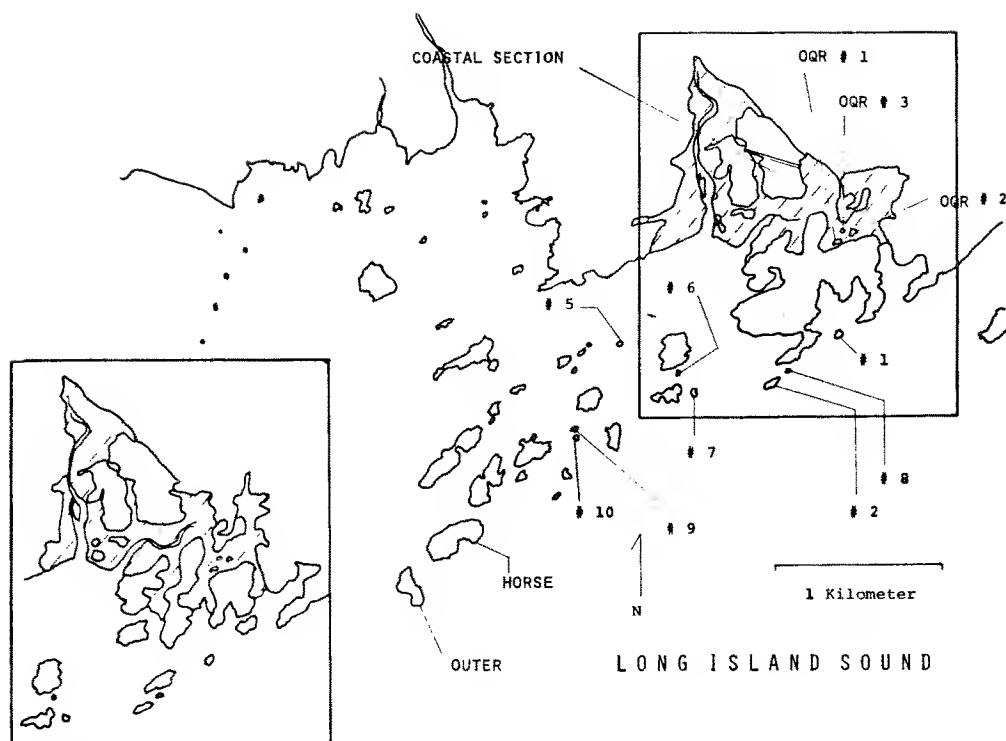


FIG. 2. Map showing the Thimble Islands and the nearby coast. Each study area is indicated. Dotted lines indicate areas of salt marsh. The inset shows the original pattern of land and salt-marsh before human alteration (after Flint, 1971).

ants were always collected, but a special effort was made to locate and collect whole colonies. This was accomplished by turning stones, logs and other objects lying on the substrate; by excavating all standing dead trees, tree stumps and fallen logs and branches; by searching the soil around the edge of exposed bedrock; and lastly, by collecting while randomly crawling and walking through the environment. Searching techniques included beating and scraping away the surface leaf litter, probing with a trowel and examining all hollows, grass tufts, rock cracks and areas of fallen twigs which were potential nest sites. An exclusively hypogean species might be missed even by such a relatively thorough survey, but in the study areas these methods were sufficient to detect even such an uncommon, hypogean species as *Amblyopone pallipes*. Along the three

transects, described later in this paper, the survey was even more intensive. Every square centimeter of leaf litter was beaten and turned, and the underlying soil surface was probed with a trowel to a depth of 5 to 10 centimeters.

Collecting was continued in each study area until one to two hours of intensive searching uncovered *no* new species, or until a full field day (4 hours intensive searching) failed to turn up more than 10% new species. On the six smallest islands, collecting always continued until the first criterion was met, and techniques employed were the same as those used along the transects.

RESULTS

Species-Area Relations

Thirty-five species of ants were found in the study areas. Twenty-eight (80%)

TABLE 1. Data on the study areas.

	Area m ²	Log ₁₀ area	Plant area m ²	Log ₁₀ plant area	Number of species of ants	Log ₁₀ number of species of ants	Distance from mainland m	Log ₁₀ distance from mainland	# open sky deciles recorded with colonies	# open sky deciles recorded w/o colonies	Plant area/number of species
1) Island # 1	3062	3.486	660	2.820	12	1.079	111	2.0453	4	-	55
2) Island # 2	4194	3.623	1632	3.213	11	1.041	282	2.4502	6	-	148
3) Island # 5	484	2.685	2.37	0.375	3	0.477	563	2.7505	-	-	0.79
4) Island # 6	161	2.207	0.25	-0.602	1	0.000	483	2.6839	-	-	0.25
5) Island # 7	968	2.986	1.68	0.230	2	0.301	483	2.6839	1	-	0.84
6) Island # 8	645	2.810	1.83	0.262	2	0.301	201	2.3031	-	-	0.915
7) Island # 9	1612	3.207	31.1	1.493	1	0.000	925	2.9661	1	-	31.1
8) Island # 10	484	2.685	3.16	0.500	2	0.301	966	2.9850	1	-	1.58
9) Horse Island	43548	4.639	33226	4.521	21	1.322	1569	3.1957	9	-	1582.19
10) Slate Transect (HI)	51.5	1.712	51.5	1.712	16 ¹	1.204	(1569)	(3.1957)	7	9	3.22 ¹
11) O.Q.R. # 1	1161	3.065	1161	3.065	17	1.230	0	-	7	-	68.29
12) O.Q.R. # 2	654	2.816	654	2.816	19	1.279	0	-	8	-	34.42
13) O.Q.R. # 3	208	2.318	208	2.318	9	0.954	0	-	4	-	23.11
14) Coastal Section	61532	4.789	61532	4.789	31	1.491	0	-	8	-	1984.90
15) Slate Transect (CS)	64.5	1.810	64.5	1.810	15 ¹	1.176	(0)	-	6	6	4.3 ¹
16) Short Transect (CS)	15.0	1.176	15.0	1.176	19 ¹	1.278	(0)	-	4	7	0.79 ¹
17) Total (except transects)	118713	5.074	99113	4.996	35	1.544	-	-	10	10	2831.8

¹ Species-area relationships recorded along transects are not strictly comparable to species-area relationships recorded from less elongate areas.

of these species were represented by one or more colonies collected; 5 (14%) were represented by stray worker ants, and 2 (6%) by stray queens alone. The number of species in the 13 study areas ranged from 1 to 30 with a mean of 10.3. With the exception of *Tetramorium caespitum* and *Myrmica americana* which are characteristic of open, dry habitats of a type not found in the Coastal Section, and of three very rare species encountered only once, all of the species occurring in the 12 island and island-in-the-marsh study areas were also present in the Coastal Section. Thus, for the most part, the ant fauna of any given island was a subset of the larger fauna present on the coast.

These 35 species include representatives of 4 subfamilies. Two of these, the Formicinae and the Myrmicinae together, account for 32 of the 35 species or 91%. A list of all the species and the study areas in which they occurred is provided in Table 2.

Species-area functions (Preston, 1962; MacArthur and Wilson, 1963, 1967; Williams, 1964; MacArthur, 1972) are drawn from the data presented in Table 1. Figure 3 relates the number of species within a study area to the variation in exposure within the study site, a parameter measured as follows: In 1972, the collection of each nest was accompanied by a subjective estimate of the amount of plant cover above the nest site, expressed as the 'per cent of the open sky visible' from the nest site. In 1973 these estimates were corroborated by means of a Forest Densimeter (Lemmon, 1956, 1957). Within the study areas as a whole, the plant cover above the ant nests varied all the way from 0% to 100%. This conveniently allowed the parameter of per cent open sky to be broken into 10 deciles (1-10%, 11-20% 91-100%) for purposes of analysis. The diversity of exposure was therefore estimated by the number of deciles of per cent open sky with which ant colonies

TABLE 2. *Ant species collected in the different study areas.*

	Island # 1	Island # 2	Island # 5	Island # 6	Island # 7	Island # 8	Island # 9	Island # 10	Horse Island	Slate Transect (HI)	O.Q.R. # 1	O.Q.R. # 2	O.Q.R. # 3	Coastal Section	Slate Transect (CS)	Short Transect (CS)
Ponerinae																
<i>Ponera pennsylvanica</i>	+								+	+	+	+		+	+	+
<i>Amblyopone pallipes</i>														+	+	+
Myrmicinae																
<i>Myrmica americana</i>								+					+			
<i>M. spatulata</i>									+		+			+	+	+
<i>M. punctiventris</i>									+			+		+	+	
<i>Aphaenogaster fulva</i>		+										+		+		
<i>A. rudis</i>	+	+							+	+	+	+		+	+	+
<i>Crematogaster cerasi</i>	+	+							+	+	+	+	+	+	+	+
<i>Solenopsis molesta</i>		+							+	+		+	+	+		
<i>Myrmecina americana</i>									+	+	+			+		+
<i>Leptothorax longispinosus</i>	+	+									+	+		+		
<i>L. curvispinosus</i>	+								+	+		+	+	+	+	+
<i>Tetramorium caespitum</i>	+	+	+	+	+	+	+		+			+				
<i>Smithistruma pergandei</i>														+		+
Dolichoderinae																
<i>Tapinoma sessile</i>	+		+		+				+	+	+	+	+	+	+	+
Formicinae																
<i>Brachymyrmex depilis</i>		+							+	+				+	+	+
<i>Camponotus castaneus</i>									+		+	+		+	+	+
<i>C. pennsylvanicus</i>											+	+		+	+	+
<i>C. ferrugineus</i>														+		
<i>C. nearcticus</i>	+								+		+		+			+
<i>Prenolepis imparis</i>	+										+	+		+	+	
<i>Lasius flavus</i>	+	+							+	+	+	+		+		
<i>L. nearcticus</i>														+		
<i>L. umbratus</i>									+	+		+		+	+	
<i>L. alienus</i>									+	+	+	+		+	+	+
<i>L. neoniger</i>	+	+	+			+		+	+	+	+	+	+	+		+
<i>Acanthomyops claviger</i>									+	+	+	+	+	+		
<i>A. latipes</i> ¹									+	+	+	+	+	+		
<i>Formica subsericea</i>		+							+	+	+	+		+	+	+
<i>F. argentea</i>														+		
<i>F. nitidiventris</i>	+	+							+				+	+	+	+
<i>F. neogagates</i>														+	+	+
<i>F. pergandei?</i>									+	+						
<i>F. rubicunda?</i>														+		
<i>F. querquetulana?</i>														+		
Total number of species:	12	11	3	1	2	2	1	2	21	15	16	19	9	31	17	18

¹ Found only in the swimming pool on Outer Island.

were associated in a study area. Thus an island with only one ant colony could have only one decile present. The frequency distribution of exposure where ants were not found, was measured every meter

along the three transects, but not in other areas. By adding up the number of deciles associated with ant colonies in each of the 10 study areas where whole ant colonies were encountered, a parameter was ob-

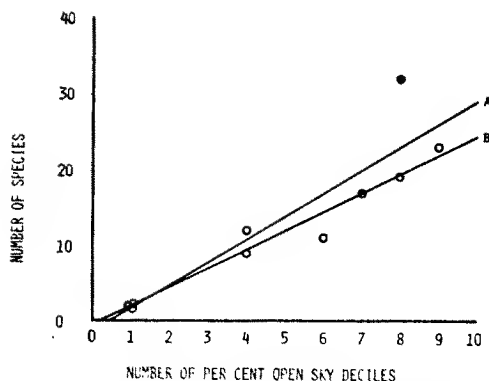


FIG. 3. The number of ant species within a study area as a function of the diversity of exposure. Diversity of exposure is scored as the number of deciles of per cent open sky associated with ant nests. Regression line A includes all 10 points; its equation is $y = 2.90X + (-1.315)$, its correlation coefficient $r = .91$. Regression line B excludes the Coastal Section (shaded circle); its equation is $y = 2.46X + (-0.411)$, its correlation coefficient $r = .98$.

tained which could be plotted against species number, as in Figure 3. The Coastal Section contained two of the transects, one 129 m long and the other 30 m long; Horse Island contained the third transect, 109 m long. All three transects were uniformly 0.5 m wide and were laid out with one end at a habitat 'edge' (the salt marsh in the case of both coastal transects, and Long Island Sound in the case of the Horse Island transect) in such a way as to cross the widest diversity of plant habitats.

The island study areas have considerable areas of bare rock (exposed bedrock) which causes their vegetated area to be considerably less than their total land area above mean high water (see Table 1). The vegetated area for each study site was determined by planimetry from an aerial photograph for the larger sites and by direct measurement for the smaller sites. Although total area and plant area are highly correlated for the islands as a whole ($r = .81$; $p < .01$), it is worthwhile to plot them separately against ant species number. The plot of species number versus total land area appears in Figure 4, and

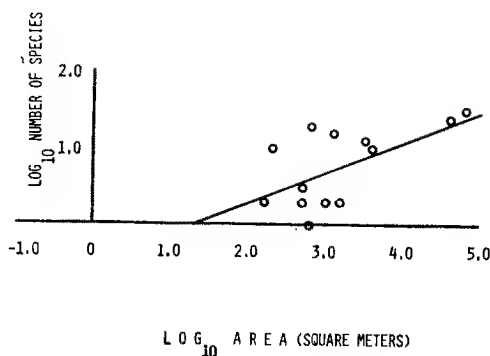


FIG. 4. The number of ant species within a study area as a function of area. $\text{Log}_{10} y = -0.508 + 0.404 (\text{log}_{10} X)$. The correlation coefficient $r = .63$.

that of species number versus plant area in Figure 5.

Species Number in Relation to Overwater Dispersal

The recent focus of attention on islands as ecological microcosms, and the proposal of the equilibrium theory of island species number (MacArthur and Wilson, 1963, 1967; Hamilton and Rubinoff, 1963; MacArthur, 1972) has led to renewed interest in the overwater dispersal abilities of organisms. It therefore seems natural to ask whether isolation-by-distance is influencing the number of ant species present on The Thimble Islands. The distance from the

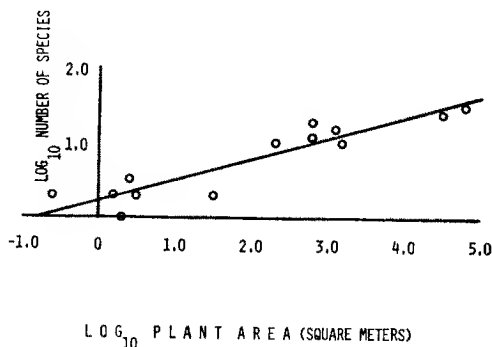


FIG. 5. The number of ant species within a study area as a function of plant area. $\text{Log}_{10} y = 0.239 + 0.272 (\text{log}_{10} X)$. The correlation coefficient $r = .93$.

coast to Horse Island, the most remote of the islands studied, is small, only 1,569 m (with a maximum overwater gap by stepping stones of 483 m), but as little is known about the dispersal abilities of most ants (Wilson, 1971), it seemed possible that isolation-by-distance may be a factor. However, several lines of evidence argue against an isolation-by-distance effect in The Thimble Islands. If this effect were at work, a unit of plant area should account for fewer and fewer species of ants as isolation increased, and plant area alone should not be able to accurately predict species number on both near and far islands. These predictions can be tested by regressing the ratio of plant area to species number for each study area against its isolation. The resulting correlation coefficient should be an estimate of the importance of the isolation-by-distance effect; a coefficient near 1 indicating that isolation is the most important factor influencing species number, and a coefficient near 0 indicating that isolation has little or no effect on species number. When this is done, the resulting correlation is $r = .20$; $p = > .50$. This means there is a greater than 50% chance that no correlation exists between these two parameters and hence that no isolation-by-distance effect is at work (by a t -test, $t = 0.687$; 11 df).

The second line of evidence comes from collections of alate queen ants made on Outer Island, which is furthest from the coast of all The Thimble Islands (Fig. 2). This island was inhabited and contained an outdoor, saltwater swimming pool which acted as a catchment area for flying insects. The pool was equipped with a filter and the water was chlorinated, so that insects falling on the surface were swept off shortly into the filter and preserved in an intact condition. On August 29 and 31, 1971, I collected living queen ants off the water surface and from the external filter, and on the 31st I also collected all the alate ants that had been trapped in the internal filter during the month of August. It was

TABLE 3. *Alate queen ants from the saltwater pool on Outer Island.*

	Number of queens recovered	Presence or absence on Outer Island	Presence or absence on other Thimble Islands surveyed
Ponerinae			
<i>Ponera pennsylvanica</i>	1	+	+
<i>Amblyopone pallipes</i>	3	-	-
Myrmicinae			
<i>Myrmica</i> sp.	1	-	+
<i>Solenopsis molesta</i>	6	+	+
Formicinae			
<i>Brachymyrmex depilis</i>	1	+	+
<i>Lasius alienus</i>	30	+	+
<i>Acanthomyops latipes</i>	1	-	-
<i>Formica subsericea</i>	1	+	+

impossible to know whether the alates found only in the filter (only *Lasius alienus* was taken on the surface of the pool) were alive when they landed in the pool. It seems reasonable however to assume that they were, as ants normally avoid stormy weather in choosing days on which to stage their nuptial flights in North America (Talbot, 1956, 1963; Kanno, 1959). Outer Island had been surveyed for ants in 1971, so that it was possible to identify the species of alates from the pool as being present or not on Outer Island. (Outer Island was not included in the discussion of species-area relations because its natural plant habitats have largely been destroyed or altered to suit the human inhabitants.) The alate queens taken from the pool and filter are listed in Table 3.

The third line of evidence bearing on the overwater dispersal capabilities of ant species comes from nuptial flights. On the afternoon of October 1, 1971, I noticed that many live winged ants were floating on the surface of Long Island Sound in the vicinity of Island # 1. Although airborne ants were not observed, it was obvious that a nuptial flight had very re-

cently occurred. The area covered by the winged ants was estimated from the position of buoys and islands to be about 26 ha. From an estimated density of four alates per m², the total estimated for the aggregation is one million. This number may at first seem high, but in fact is quite believable in light of the known high population density and large alate production of ant colonies (Wilson, 1971). Several hundred alates were collected from different parts of the 26 ha area, and most were still viable enough to crawl actively once they had been removed from the water. Of the ants seen or collected, it is estimated that at least 20% were females, so that the flight must have represented a very large number of potential propagules—on the order of 200,000. Within the area, the queens did not seem clumped together, but rather freely dispersed among the males. Of the 51 alate queens actually collected from this flight, 43 were *Acanthomyops claviger*, 7 were *Lasius alienus*, and 1 was a *Myrmica* species. The October 1 flight date for the queens of *Acanthomyops claviger* and *Lasius alienus* agrees with information in the most recent revisions of these genera (Wing, 1968; Wilson, 1955).

The area covered by the ants included Island # 1, a study area in which thorough surveys in 1971 and 1972 failed to detect the presence of *Acanthomyops claviger*, *Lasius alienus*, or of any species of *Myrmica*. The *Acanthomyops* and the *Lasius* species were however both quite common in coastal habitats only a few hundred meters away from Island # 1, where at least two species of *Myrmica* could also be found. It was not possible to land a boat on Island # 1 at that time, but unless the alates avoided land, about 12,000 alates should have fallen on Island # 1's 3000 m² of area, as the sea around it on all sides was covered with alates at about 4 per m². If only 10% of all the alates were queens, and if the proportions present in my collection are at all representative of the actual proportions of species in the flight, then about 1000 *Acanthomyops* queens,

150 *Lasius* queens, and 20 *Myrmica* queens should have fallen on Island # 1. Yet, even with such a high immigration rate, neither the *Acanthomyops* nor the *Lasius* were able to maintain a single colony on Island # 1 (or on any other small to medium sized island featuring xeric conditions). These facts point to exclusion due to habitat inadequacy rather than to low immigration rates.

Ant Life on Small Islands—Species Turnover from 1971 to 1972

From Figure 5 it can be seen that the study areas break fairly naturally into three groups based on their plant area. The six islands with a plant area less than 30 m² are of unusual interest because their tiny area of habitation allows all ant species present to be detected with a high degree of certainty, and their small size and rocky, xeric environments suggest that they are only a marginally suitable ant habitat. These islands were censused largely by crawling and probing with fingers, trowel and forceps through all of the pebbly soil present in narrow, shallow cracks in the bedrock. The rest of these islands (better than 99% of their area) consisted of smooth, exposed granite supporting only lichens, and ants were never present on this bare rock unless a crack with vascular plants growing in it lay nearby.

Typical vegetation of these small, barren islands comprised a number of salt-tolerant grasses (e.g., *Distichlis spicata*), herbs like seaside goldenrod (*Solidago sempervirens*), and woody shrubs like poison ivy (*Rhus radicans*). The surface area of soil was less than that of plants, as the plants tended to spread their leaf area laterally beyond the bounds of the rock cracks they were rooted in. This fact means that the total area to be searched for ants was very small, a factor which added to the reliability of the census. Table 4 presents data on the six smallest islands along with the per cent faunal turnover from 1971 to 1972. Faunal turnover is calculated as follows: The total number of species

TABLE 4. Turnover of ant species on six small islands 1971-1972. + indicates that a species is present in a given year, while a blank indicates that it is absent.

	Island # 5		Island # 6		Island # 7		Island # 8		Island # 9		Island # 10	
	1971	1972	1971	1972	1971	1972	1971	1972	1971	1972	1971	1972
Species												
<i>Ponera pennsylvanica</i>									+			
<i>Myrmica americana</i>											+	+
<i>Leptothorax curvispinosus</i>	+		+									
<i>Tetramorium caespitum</i>	+	+		+	+	+		+	+	+		
<i>Tapinoma sessile</i>		+	+		+	+						
<i>Lasius neoniger</i>	+	+					+	+			+	+
Species number	3	3	2	1	2	2	1	2	2	1	2	2
Per cent turnover	33		100		0		33		33		0	
Average per cent turnover = 33%												

present in 1971 but absent in 1972 was added to the total number absent in 1971 but present in 1972 for each island. This sum was then divided by the total number of species recorded from that island during the whole two-year period. The average value of species turnover in one year for these six islands is 33%, a very high figure, and one which has great implications for the character of ant life on these small islands. Larger islands were excluded from consideration of species turnover because their much larger plant area precluded the kind of total census this type of analysis requires.

DISCUSSION

Species-Area Relations

Since the work of MacArthur and Wilson (1963, 1967) and Williams (1964) attention has been focused on the regular relationship between the size of the area sampled and the number of species of a given taxon encountered. It has also repeatedly been said that area itself is only a rough approximation to the spatial distribution of environmental conditions which provide opportunities for species to exist. Little is known as yet about those environmental features which actually control the

diversity of species of a given taxon. The study by G. E. Watson (1964) which showed that the number of species of passerine birds inhabiting Aegean Islands is best correlated with the number of identifiable island habitats is a notable exception. But even Watson's work describes the distribution of birds in terms of large plant associations and gross morphological features of the abiotic environment, and not in terms of the actual parameters which are important to the birds.

It has been shown (Goldstein, unpubl.) that the ants of the Branford-Guilford study areas all have species-specific ranges of exposure (proportions of sun and shade) in which they occur. These regimes of exposure are also temperature regimes, with maximum surface temperature increasing 2.4F. with every 10% increase in per cent open sky on Horse Island, and 8.4F. with every 10% increase in per cent open sky in the more sheltered Coastal Section. It has been known for some time (Talbot, 1934; Goesswald, 1938, 1941) that the ability of ant species to tolerate high temperature and concomitant low humidity varies greatly, and that ants characteristic of hot, dry habitats are far more tolerant of hot, dry conditions than ants which

normally occur in cool, moist habitats. These physiological insights have not been used before to make biogeographical predictions or predictions concerning the species-area relationship. It can be seen from the data presented in Table 1 and Figure 3, that the greater the range of exposure (and hence, the more temperature regimes) a study area contains, the more ant species it contains. This relationship is very nearly linear ($r = .98$; $p < .001$), if the Coastal Section (the closed circle in Fig. 3) is excluded from the correlation. The rationale for excluding this point is based on a crucial effect of scale. The Coastal Section is large enough in area to include a number of relatively rare species (it contains five species not known from any other study area). There is therefore a threshold of area, above which the number of temperature regimes is not adequate to predict the maximum number of species of ants that an area will contain. Above 3 or 4 ha (The Coastal Section is about 6 ha) the total species count reflects the presence of rare species which increase in number as area increases due to factors other than the increase in the number of temperature regimes.

Those factors actually controlling the distribution of rarer ant species in the study areas can only be guessed at, at this time. If we include the Coastal Section in the correlation, the coefficient is reduced ($r = .91$; $p < .001$), and the overall correlation is significantly different as tested by the method of Bryant (1960) (for $r = .98$ and $r = .91$, $Z = 2.4878$; $p < .05$).

Looking at Figures 4 and 5 it is interesting to note a sizable difference in the slope of the regression lines (fitted by least squares), as well as a large and highly significant difference ($Z = 4.5849$; $p < .001$) in the values of the correlation coefficients, between the two functions. MacArthur and Wilson (1967) have laid considerable stress on the limited range of slopes that species-area plots on log-log axes have shown. On islands, most are between 0.20 and 0.35, while non-isolated areas of dif-

ferent sizes on continents show much lower slopes when plotted in this way. Total area, which is less well correlated with species number (Fig. 4) than plant area, yields an abnormally high slope value (0.40) on a log-log plot. But in the present study, when plant area is plotted against ant species number, the slope of the regression line (Fig. 5) has a value (0.27) right in the middle of the range of values reported by other workers and predicted from the lognormal distribution of relative species abundance (MacArthur and Wilson, 1967). Thus it seems that the problem often encountered in species-area relations, namely that the relationships do not hold for small areas, can be surmounted by identifying and measuring the relevant parameters.

Aggressive interactions typical of the ant communities studied by some earlier workers (Yasuno, 1965; Brian et al., 1966) were not observed in this study, but these prior studies were all conducted in grassland or heath with very regular habitat structure, while the present study was conducted in an area of very complex physical and biotic environment.

Species Number in Relation to Overwater Dispersal

No evidence has been found in this study to suggest that distant islands have fewer ant species than predicted by their plant area or the diversity of their exposure to the sun. Medium-sized true islands have fewer species than do less exposed (to wind and salt spray) islands in the marsh of the same plant area, but all evidence points to this being due to habitat differences resulting from exposure. Species absent from these islands have been shown to be available for colonization in large numbers, and even on the more distant islands, species are present when appropriate habitats are present for them (see Table 2). Furthermore, there is evidence (Table 3) of immigration of species that do not maintain themselves on the islands surveyed onto even the outermost (Outer) island, also

implying that absence is due to habitat unsuitability.

*Ant Life on Small Islands—
Species Turnover from 1971 to 1972*

The concept of the species equilibrium introduced by MacArthur and Wilson in 1963 and elaborated by them in 1967 (see also Wilson, 1969; MacArthur, 1972) states that species number can best be thought of as a balance between immigration and extinction. Immigration in the form of arriving propagules has been extremely difficult to measure. Propagules themselves are often not detectable, and neither is their subsequent disappearance. But it is not absolutely necessary to measure this constantly changing pool of propagules. For most biological purposes it suffices to record only immigrants which become established and so are repeatedly recorded during a reasonable time interval. Similarly, one need record the extinction (disappearance) only of those species which have actually been established for some reasonable period of time.

In light of this, attention has been focused on the pattern of appearances and disappearances of species on islands. Three major studies on this subject are those of Jared Diamond (1960, 1972) on the avifaunas of the California Channel Islands and of Karkar, New Guinea, and that of Wilson and Simberloff (1969), Simberloff and Wilson (1969), and Wilson (1969) on the recolonization of experimentally 'defaunated' mangrove islands in the area of The Florida Keys. Wilson and Simberloff did not emphasize the turnover of species, but rather concentrated on the number of species present on an island at equilibrium. Diamond, however, estimated the minimum turnover rate of species of land birds on the California Islands from 1917 to 1968 as varying between 17 and 62% for different islands (Diamond, 1972). He then went on to show that the turnover rate for tropical Karkar over a similar 49-year period was approximately the same. The turnover rate for both, he reports as vary-

ing between 0.33 and 1.22 percent per year. In contrast the six smallest islands in The Thimbles Chain, showed a combined species turnover rate of 33% in one year with the turnover on individual islands ranging from 0% to 100% (Table 4). These strikingly high rates require comment.

In the ecological literature dealing with territoriality, "marginal" (as opposed to "optimal") habitats are usually defined as sites where animals suffer lowered reproductive success. Although little is known about colony age at reproduction in ants, it is known that most colonies do not reproduce in the first 1-3 years, and that as much as 8-10 years may be required for colony growth before alates will be produced in a cool climate (Brian, 1957). Brian has also shown that in Scotland, ant colonies that are located in habitats which are marginal due to their coolness may survive for some years without ever reproducing. While carrying on this analogue of vegetative growth in plants, such colonies exhibit the normal patterns associated with food gathering, trophallaxis and the rearing of brood.

Apparently most of the ants on the smallest Thimble Islands are in this category. They either never assimilate enough biomass to reproduce (virgin alates were never detected on any of these islands), or else the rigor of their exposed, rocky environment is such that the likelihood of an unusual abiotic event causing colony extinction prior to reproduction is very high.

The average turnover rate of 33% suggests that these smallest islands are marginal habitats but that ants have (as the nuptial flight observations suggest) a high immigration rate. It is not strictly comparable to the island avifauna turnover rate mentioned above because in a sense the ants on these smallest islands never become established and hence cannot go extinct. On the other hand, the basic principle which underlies the high rate of species turnover on islands—that species populations are small (MacArthur and Wilson, 1967)—holds for the inability of these

island ants to establish themselves as reproductive populations. In the case of the island birds which go locally extinct, it is presumed that in a fluctuating environment a point was reached where the total energy that any local species population could assimilate was inadequate to retain a single pair of breeding individuals. Extinction, as Williams (1964) has pointed out, occurs at the point where any species population falls to a single unfertilized individual. The population of ants on the six smallest Thimble Islands, which never include more than a single colony per species, are limited to the point where they are not observed to reproduce. Whether this is due to inadequate food supply or to frequent mortality due to abiotic factors, an ant colony which survives but does not produce alates is strictly analogous to an inseminated female vertebrate which is too starved to reproduce. It is interesting that this peculiar "vegetative," non-reproductive presence of the ants may go on for at least a year and presumably longer.

SUMMARY

A survey of ants was conducted on a small chain of coastal islands and in nearby mainland areas in New Haven County, Connecticut in 1971 and 1972. Ecological data collected with each ant colony in 1972 show that the diversity of exposure to the sun of habitats occupied by ants is the best predictor of the number of species in study areas up to 4 ha in extent. The total area of the study area is a relatively poor predictor of the number of species a site will contain. The plant area of the study areas is a far better predictor of species number, although not as good as the diversity of exposure of habitats. Thus a habitat characteristic which has been identified as crucial to ant species distributions—the temperature regime associated with a given range of shadiness—is of predictive value in explaining the species-area relationship for ants.

The hypothesis that species absent on the islands are missing due to problems of

overwater dispersal (isolation-by-distance) is rejected based on collections of alate ants from the most isolated island, and on other nuptial flight observations.

The six smallest islands which contained one to three species of ants and were judged to be marginal ant habitats, were comprehensively surveyed in 1971 and 1972. These were found to have the very high average species turnover rate of 33% in one year suggesting that the earlier judgement that these are marginal ant habitats is correct.

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